Gall wasp community response to fragmentation of oak tree species

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Gall wasp community response to fragmentation of oak tree species: importance of fragment size and isolated trees

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Abstract. We explore the impact of habitat fragmentation on interactions between keystone resources of forest trees—oaks, genus *Quercus* (Fagaceae)—and an associated radiation of specialist cynipid gall wasps. Habitat fragmentation is predicted to have bottom-up impacts on cynipid communities through impacts on host plant quality (plant vigor hypothesis). We explored the bottom-up impacts on cynipid communities of habitat fragment size, fragment edge effects and presence of isolated oaks. We quantified temporal and spatial variation of leaves produced in the canopy to quantify plant vigor, and surveyed cynipid gall species abundance and richness over three years using 15 permanent forest patches and 25 isolated oaks in a fragmented oak woodland landscape in central Mexico. Cynipid gall abundance and species richness were higher in isolated oaks and small woodland fragments than in larger ones. Cynipid abundance and species richness were also higher along fragment edges in comparison with fragment interiors. This contrasts with patterns observed in other taxa. In addition, host plant quality was higher in isolated trees, in smaller fragments and along fragment edges. We therefore hypothesize that observed patterns in cynipid abundance and species richness are driven by changes in host plant quality due to forest fragmentation. Our data represent a baseline for longer-term monitoring of fragmentation effects at a landscape scale. Further work is required to explore alternative potential explanations for observed patterns, including the estimation of potential top-down impacts of fragmentation mediated by natural enemies.

Key words: cynipids; edge effect; habitat fragmentation; isolated trees; Lake Cuitzeo basin; oak gall wasps; plant vigor; *Quercus*.

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INTRODUCTION

Oaks (*Quercus* species) are dominant late successional species in a wide range of habitats and offer key environmental services (i.e., carbon sequestration, energy production and water cycle regulation) (Faivre-Rampant et al. 2011). Oaks support characteristic and species-rich assem-

blages of associated organisms, particularly herbivorous insects (Tews et al. 2004, Tovar-Sánchez and Oyama 2006*a, b*). Of these, the most specialized include the cynipid gall wasps (Hymenoptera: Cynipidae: Cynipinae). Each gall wasp is specific to a single oak species or higher taxonomic section (Nieves-Aldrey 2001, Stone et al. 2009). For example, very few cynipids that induce galls on white oaks (*Quercus* section *Quercus*) also induce galls in other taxonomic sections (e.g., red oaks, section Lobatae) (Abrahamson et al. 2003) and evolutionary shifts of gall wasps between oak sections are extremely rare (Stone et al. 2009). Cynipids are a useful model system in examining patterns of insect herbivore species richness and distribution due to their species richness and host specificity (Hayward and Stone 2005). An important feature of some oak-cynipid systems is the ability of some oak species to support very rich communities, providing considerable resolution for analysis of habitat-associated changes in assemblage structure. Examples include *Quercus turbinella* in North America, which supports 20 species of cynipids wasps and *Quercus robur* and *Quercus petraea* in Europe, which support more than 70 species (Fernandes and Price 1988, Csóka et al. 2005). Such host plant species have been called "super-hosts" (Araùjo et al. 2013). Here, we analyze oak cynipid assemblages associated to "super-hosts" species to examine the impact of habitat fragmentation on Mexican oak communities.

In Mexico, oak forests have been highly fragmented because of the great economic importance of the trees (Valencia-Ávalos and Nixon 2004). Masera et al. (1997) have estimated that 167,000 ha/yr of temperate forests are lost, resulting in an annual deforestation rate of 0.64% in Mexico. An extreme consequence of habitat fragmentation is the isolation of individual trees, which may then represent refuges and keystone resources to herbivorous insects (Hanski and Gilpin 1997, Tews et al. 2004, Manning et al. 2006, Müller and Goßner 2007, Fischer et al. 2010). Such isolated trees enhance the connectivity among forest fragments and aid their regeneration (Manning et al. 2006).

Specialized biotic interactions associated with keystone resources are seriously affected by habitat fragmentation (Tews et al. 2004, Wang et al. 2005, Rodríguez-Cabal et al. 2010). Forest fragmentation can modify the composition, abundance and distribution of herbivores such as gall inducing insects (Didham et al. 1996, Chust et al. 2007, Ruiz-Guerra et al. 2010, Kaartinen and Roselin 2011). In general, habitat fragmentation affects herbivore diversity through their biotic interactions (Tscharntke 1992, Didham et al. 1996, Fagan et al. 1999) with natural enemies (top-down effects) (Holt 1996, Stone et al. 2002, Askew et al. 2013) and host plants (bottom-up effects) (Tscharntke et al. 2002). Holt (1996) developed models showing that higher trophic level species such as parasitoids should be more vulnerable to the effects of habitat fragmentation than herbivorous insects due to their higher requirements of energy and area in the forest (see also Tscharntke et al. 2007). The release of herbivores from top-down control in habitat fragments can thus benefit local populations (Kruess and Tscharntke 1994). Gall wasp populations are strongly influenced by top-down effects (Stone et al. 2002), with most studies showing high mortality through attack by chalcid parasitoids (Moriya et al. 1989, Stone et al. 2002, Askew et al. 2013). If top-down effects have a strong impact on gall wasp community structure, habitat fragments could support relatively enriched gall inducer communities by providing relatively enemy-free space.

Habitat fragmentation may also influence gall inducer population and community dynamics through bottom-up effects on host plant preference (Yamasaki and Kikuzawa 2003, Ruiz-Guerra et al. 2010) and quality. Habitat fragments experience a suit of environmental changes, which are even stronger along the fragment edges (Saunders et al. 1991, Murcia 1995). Certain plants are adapted to the conditions provided by continuous forest (i.e., higher humidity, lower temperature, photosynthetically active radiation and wind speed) (Young and Mitchell 1994, Chen et al. 1995). However, changes in abiotic conditions due to fragmentation may be stressful for these plants (Fernandes and Price 1988), reducing plant vigor (i.e., reduction in growth rate, and production of leaves, shoots and reproductive structures) (Price 1991, Saunders et al. 1991, Prada et al. 1995). Some studies show that gall inducing insects prefer vigorously growing plants or plant mod-

ules (e.g., leaves or shoots) (Price 1991, Preszler and Price 1995, Cornelissen et al. 2008), hence, it is expected that gall inducing insects are less abundant or diverse in small patches if plants are more stressed.

The effects of habitat fragmentation on populations of gall inducing insects are poorly known (but see Chust et al. 2007) and few long-term studies have analyzed gall inducing insect interactions (Santos et al. 2008). Studies to date show no consistent response of gall inducing insects to habitat fragmentation; in some cases, gall abundance increases with habitat fragmentation (Wang et al. 2005, Chust et al. 2007), but in others, no relationship has been found (Julião et al. 2004, Dunley 2009). High regional species richness of oak gall wasps, combined with ease of sampling make gall wasps a suitable taxon for quantifying impacts of habitat fragmentation (Kinsey 1937, Pujade-Villar et al. 2009, Nieves-Aldrey et al. 2012). Our study documents biotic interactions over three years. We studied the spatial and temporal variation of gall wasp diversity and plant vigor across oak fragmented populations, to quantify the importance of fragment size, edge effects and isolated oaks on gall abundance and diversity in a fragmented landscape in Mexico. We hypothesize that habitat fragmentation will have a strong impact on gall wasp community structure, where most fragmented habitats will support enriched gall wasps communities. A second hypothesis proposes that isolated oaks represent key resources for gall wasps, having higher richness and abundance of gall wasps in isolated trees than in forest fragments. Finally, we expected that plant vigor (canopy cover) will be negatively influenced by habitat fragmentation affecting in turn gall wasps diversity.

Methods

Study location

This study was conducted in the Lake Cuitzeo basin, a hydrological unit with an area of 4026 km^2 located in Michoacán state, Mexico. It is located in the physiographic province of the Transmexican Volcanic Belt. The basin contains the Lake of Cuitzeo with a wetland of approximately 300 km^2. The basin is representative of the environmental and socioeconomic conditions of central Mexico and has experienced strong fragmentation resulting in a highly fragmented landscape forming a mosaic of scrubland, forests (mainly pine, oak and mixed forests) and agricultural lands (López et al. 2006). The basin includes Morelia, the state capital of Michoacán state, for which urban area grew six-fold between 1975 and 2000 (López et al. 2001). Land cover and land use change analyses indicate that the period 1986–1996 was characterized by high rates of deforestation and forest degradation throughout the basin (Mendoza et al. 2011) due to strong human pressures including urban growth, expansion of the agricultural frontier and the removal of trees for charcoal production (López et al. 2006, Aguilar et al. 2012, Castillo-Santiago et al. 2013). Consequently, large continuous oak populations have been reduced to a many small patches of variable size.

Fragmentation of oak forests and selection of sampling sites

Michoacán state has a very high deforestation rate of approximately 1.8% per year over 18 years (Bocco et al. 2001). Remaining oak forests in the Lake Cuitzeo basin have previously been characterized into 1241 fragments of different sizes (López et al. 2001). We selected 15 permanent forest fragments which were divided equally among three size categories: (1) five small ($\leq$4 ha) forest fragments; (2) five medium-sized (4–12 ha) forest fragments; and (3) five large (>12 ha) forest fragments. We also selected 25 individual oak trees isolated by distances of at least 400 m from surrounding forest (see Appendix: Fig. A1). The oak species present at each sampling site are shown in Table A1.

Study system and sampling

Cynipid gall wasps induce structurally complex galls on various oak tissues (Hayward and Stone 2005). Most oak gall wasp life cycles involve strict alternation between two generations: a sexual generation gall develops in the spring or early summer, while an asexual generation develops during the summer and autumn, usually during the same year (Stone et al. 2002). Oak gall wasp taxonomy is problematic, and adults of the two generations are so different morphologically that they have sometimes been described as different species, occa-

sionally even in separate genera (Pujade-Villar et al. 2001). Nevertheless, galls from each generation can usually be identified unambiguously on the basis of characteristic morphology, location on the tree and oak host taxon (Stone et al. 2002, Stone et al. 2009).

Gall surveys were conducted monthly from September 2007 to October 2010. At each study site, we established two parallel 5 × 50 m transects, one located on the fragment edge and one in the fragment interior (average distance of 115 m from forest border). In each transect, we recorded oak density and oak species richness. To determine the effects of habitat fragmentation on these measures, we used a generalized linear model (GLM) analysis for each response variable, using a Poisson error distribution and log link function. An LSMeans test was used for a posteriori comparisons (SAS 2000).

We recorded monthly cynipid gall abundance and species richness on each individual oak tree. Gall sampling incorporated the full height of each canopy, through collection of three branches from each of top, intermediate and bottom strata of each tree, following Cuevas-Reyes et al. (2004). We verified that each distinct gall morphology collected was induced by a different gall wasp taxon by rearing galls in the laboratory and identifying the adult to genus and to morphospecies. For ecological studies of gall inducing insects, morphospecies has become an acceptable substitute for species, assuming that each gall morphospecies is unique to a particular gall inducing insect (Stone and Schönrogge 2003, Cuevas-Reyes et al. 2004, Cuevas-Reyes et al. 2011). Gall wasps can then be identified on the basis of their characteristic gall morphology, location on the oak, and oak host taxon (Abrahamson et al. 1998, Stone et al. 2002, Stone et al. 2009). Samples of all gall species collected are preserved in a dry collection at the Museo Nacional de Ciencias Naturales, Madrid (Spain) and the Laboratorio de Ecología Genética y Molecular, CIEco, UNAM (Mexico), awaiting formal taxonomic identification.

The surveys and analyses were separated into spring and autumn generations on the basis of phenology and wasp morphology to reduce issues of non-independence associated with having one or both generations of a single species in the same analysis (Bailey et al. 2009). We used a GLM to test differences in gall richness between all oak species. To determine the effects of fragment size and distance to the edge on gall wasp species richness and abundance, we performed a GLM. The model used a Poisson error distribution and log link function. An LSMeans test was used for a posteriori comparisons (SAS 2000). We also analyzed overall changes in community composition in response to the fragment size and isolated oaks using a permutational multivariate ANOVA (Permanova; Anderson 2005) for oak and gall wasp community composition using species richness, McIntosh diversity index and oak abundance or gall abundance. To examine whether differences in species richness of gall wasps between fragment sizes were driven by differences in gall abundance, we constructed rarefaction curves for each fragment size and estimated cumulative species per tree using EstimateS 9.1.0 (Colwell 2011).

Plant vigor.—Plant vigor was quantified as numbers of leaves produced in the canopy (Prada et al. 1995, Faria and Fernandes 2001). This is probably an appropriate measure for gall wasps, many of which induce their galls on these organs or associated buds and shoots (Price 1991, Fritz et al. 2003). In each transect, we marked the adult trees of each species and in each survey we classified leaf canopy cover according to the proportion of trees in each of four production categories: (1) 0%; (2) 1–25%; (3) 26–50% and (4) 51–100%, following Williams et al. (1997). We used a GLM to determine the effect of fragment size on plant vigor. The same analysis was conducted to determine the differences in plant vigor between transects. The analysis used a binomial distribution and a logit link function. A linear regression analysis was used to determine the relationship between gall abundance and percentage of canopy cover, for each fragment size and isolated oaks.

Results

General description of the oak-gall community

Over all fragment types (isolated oaks, small, medium-sized and large fragments), we sampled ten *Quercus* species. In total, our surveys incorporated 179 trees of five species in the white oak section *Quercus* (*Q. laeta, Q. obtusata, Q. deserticola, Q. magnoliifolia* and *Q. glaucoides*) and 206 trees

Table 1. Differences in oak gall wasp species richness in oak "super-hosts" species. GENMOD procedure (SAS 2000) was applied for modelling log function to each plant species. Different superscript letters after values indicate significantly different means. Values in boldface show the maximum for each oak species and metric. Values shown are means with 1 SE in parentheses.

Host plant	Isolated trees	Small fragments	Medium-sized fragments	Larger fragments	χ^2	P
Q. obtusata	**13.3**^{A} (±0.8)	5.1^{B} (±0.9)	2.4^{C} (±0.9)	1.6^{C} (±0.7)	8.1	<0.04
Q. castanea	**12.7**^{A} (±1.2)	5.2^{B} (±0.5)	3.5^{C} (±0.5)	1.1^{C} (±0.5)	28.3	<0.001
Q. deserticola	**10.8**^{A} (±0.8)	4.8^{B} (±0.6)	4.1^{B} (±0.7)	1.8^{C} (±0.5)	11.9	<0.007

of five species in the red oak section *Lobatae* (*Q. castanea*, *Q. scythophylla*, *Q. candicans*, *Q. dysophylla* and *Q. crassifolia*). All except *Q. crassifolia* hosted cynipid galls. Over three years, we sampled a total of 5843 galls, comprising 1336 spring generation galls and 4507 autumn generation galls. We identified 105 distinct gall morphotypes, of which 69 (65.7%) were induced on leaves (14 spring and 55 autumn generations), 8 (7.6%) on leaf petioles (6 spring and 2 autumn generations), 20 (19%) on stems (8 spring and 12 autumn generations), 7 (6.7%) on buds (all autumn generation) and 1 (1%) on catkins (spring generation).

Oaks species richness and host-plant density

Oak species richness did not differ significantly among forest fragment size categories ($\chi^2 = 0.4$, df = 3, $P = 0.8$) or between edge and internal transects in each fragment ($\chi^2 = 0.5$, df = 1, $P = 0.9$). Similarly, we found no differences in host plant density among forest fragment size categories ($\chi^2 = 0.04$, df = 3, $P = 0.9$) or between edge and internal transects in each fragment ($\chi^2 = 0.08$, df = 1, $P = 0.9$). These results were supported by Permanova analysis of oak communities, which showed diversity, richness and density to be similar between all fragments (Permanova: density: $F = 0.47$, $P = 0.6$; richness: $F = 0.8$, $P = 0.4$; McIntosh diversity index: $F = 0.1$, $P = 0.9$).

Oak gall wasp diversity patterns

Oak gall wasp species richness differed among oak species. *Quercus obtusata*, *Q. castanea* and *Q. deserticola* may be considered "super-hosts" because they supported most of the gall species richness (Table 1) and abundance (Table 2). Oak gall wasp richness was significantly higher in *Q. obtusata* (40 gall species), *Q. deserticola* (25) and *Q. castanea* (33), in comparison with *Q. candicans* (8), *Q. scythophylla* (8), *Q. magnoliifolia* (7), *Q. glaucoides* (7), *Q. dysophylla* (2) and *Q. laeta* (2) ($\chi^2 = 46.1$, df = 8, $P = 0.0001$).

We found a similar pattern of oak gall wasp species richness in both gall generations (Fig. 1). Isolated trees had higher gall wasp species richness (spring: 2.7 ± 0.3; autumn: 3.1 ± 0.4) than trees in small (spring: 1.7 ± 0.2; autumn: 2 ± 0.1), medium-sized (spring: 1.5 ± 0.11; autumn: 2.1 ± 0.2) and large (spring: 1.3 ± 0.1; autumn: 1.58 ± 0.1) forest fragments (spring: $\chi^2 = 19.8$, df = 3, $P = 0.0002$; autumn: $\chi^2 = 13.3$, df = 3, $P = 0.004$). There were no significant differences in gall species richness between generations in each fragment size ($\chi^2 = 12.7$, df = 1, $P = 0.3$) (Fig. 1A). Gall species richness was higher in fragment edges (spring: 1.6 ± 0.1; autumn: 1.73 ± 0.08) than in fragment interiors (spring: 1.9 ± 0.16; autumn: 1.43 ± 0.1) (spring: $\chi^2 = 16.43$, df = 1, $P = 0.013$; autumn: $\chi^2 = 11.21$, df = 1, $P = 0.02$). Both gall generations showed similar contrasts between fragment edge and interior ($\chi^2 = 0.98$, df = 1, $P = 0.4$) (Fig. 1B).

Table 2. Differences in oak gall wasp abundance in oak *"super-hosts"* species. GENMOD procedure (SAS 2000) was applied for modelling log function to each plant species. Different superscript letters after values indicate significantly different means. Values in boldface show the maximum for each oak species and metric. Values shown are means with 1 SE in parentheses.

Host plant	Isolated trees	Small fragments	Medium-sized fragments	Larger fragments	χ^2	P
Q. obtusata	**26.8**^{A}(±4)	8.1^{B} (±1.3)	8.1^{B} (±1.3)	5.1^{C} (±1.6)	16.2	<0.005
Q. castanea	**21.3**^{A} (±5)	17.1^{B} (±3.0)	5.1^{C} (±4.0)	4.9^{C} (±3.0)	21.1	<0.0001
Q. deserticola	23.3^{C} (±9)	**45.3**^{B} (±6.0)	9.8^{C} (±3.0)	5.3^{D} (±7.0)	4.2	<0.03

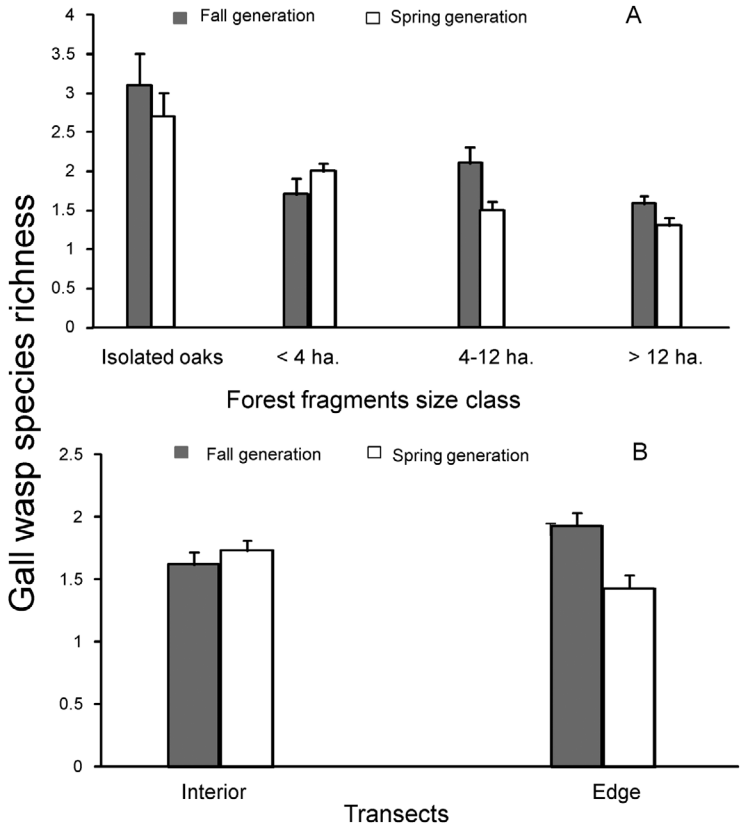

Fig. 1. Impacts of fragment size and interior/exterior transect location on gall species richness, by generation. (A) Effects of fragment size, including isolated oaks. (B) Comparison between interior and edge transects in each fragment. Untransformed data are shown.

Gall abundance (Fig. 2) was higher in isolated oaks (spring: 21.39 ± 25; autumn: 41.0 ± 5) than on trees in small (spring: 14.0 ± 6; autumn: 7.45 ± 2.6), medium-sized (spring: 7.1 ± 2.0; autumn: 14.25 ± 3.5) and large forest fragments (spring: 4.8 ± 2.1; autumn: 7.7 ± 2.6) (spring: $\chi^2 = 1567$, df = 3, $P = 0.0001$; autumn:$\chi^2 = 174.6$, df = 3, $P = 0.0001$). Isolated trees also showed higher abundance of autumn generation than spring generation galls ($\chi^2 = 9.4$, df = 1, $P = 0.003$) (Fig. 2A). As for species richness, gall abundance was higher in fragment edges (spring: 10.77 ± 1.7; autumn: 13.19 ± 1.6) than in fragment interiors (spring: 6.6 ± 2; autumn: 7.8 ± 1.4) (spring: $\chi^2 = 31.6$, df = 1, $P = 0.0001$; autumn: $\chi^2 = 359.3$, df = 1, $P = 0.0001$), again with no difference in pattern between gall generations ($\chi^2 = 5.5$, df = 1, $P = 0.5$) (Fig. 2B).

These results were supported by Permanova analysis, which showed gall community diversity, abundance and richness in each generation to be higher in isolated oaks and small fragments than in larger forest fragments (Abundance: spring: $F = 4.7$, $P = 0.004$, autumn: $F = 8.5$, $P = 0.001$. Richness: spring: $F = 3.2$, $P = 0.05$, autumn: $F = 11.3$, $P = 0.03$. McIntosh diversity index: spring: $F = 6.8$, $P = 0.01$, autumn: $F = 11.6$, $P = 0.001$). Rarefaction curves showed that the observed differences in cumulative species richness persisted even when samples were rarefied to similar abundances of individuals (Fig. 3).

Plant vigor

We found significant differences in oak tree vigor (as measured by leaf canopy cover) among fragment size classes. Leaf production was significantly higher in isolated oaks (69.7 ± 3.5) in comparison with small (48.3 ± 1.2) medium-sized (45.9 ± 1.4) and large fragments (44.1 ± 1.1) ($F = 21.3$, df = 3, $P = 0.0001$). We also found

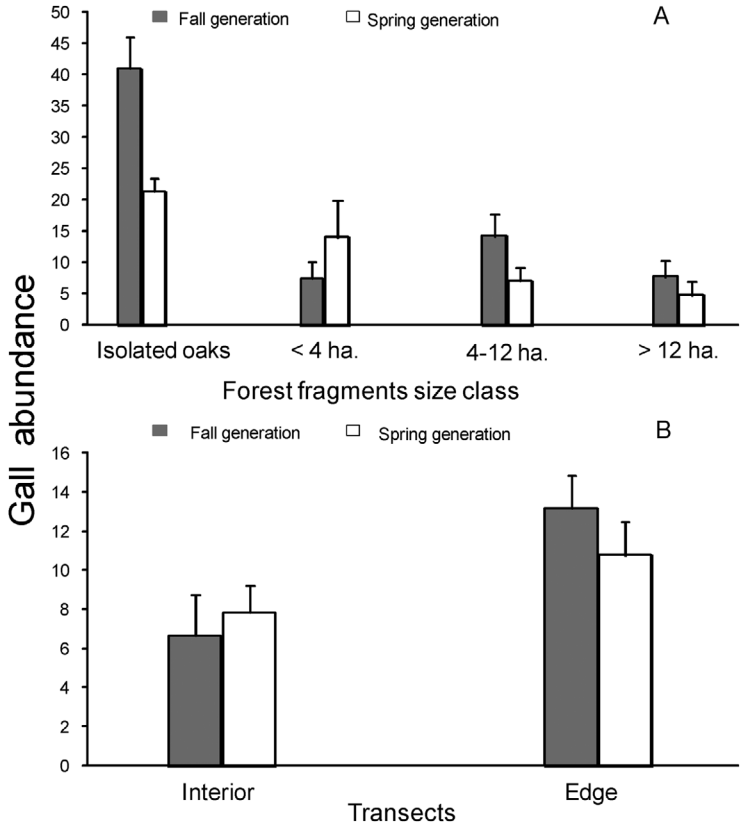

Fig. 2. Impacts of fragment size and interior/exterior transect location on gall abundance, by generation. (A) Effects of fragment size, including isolated oaks. (B) Comparison between interior and edge transects in each fragment. Untransformed data are shown.

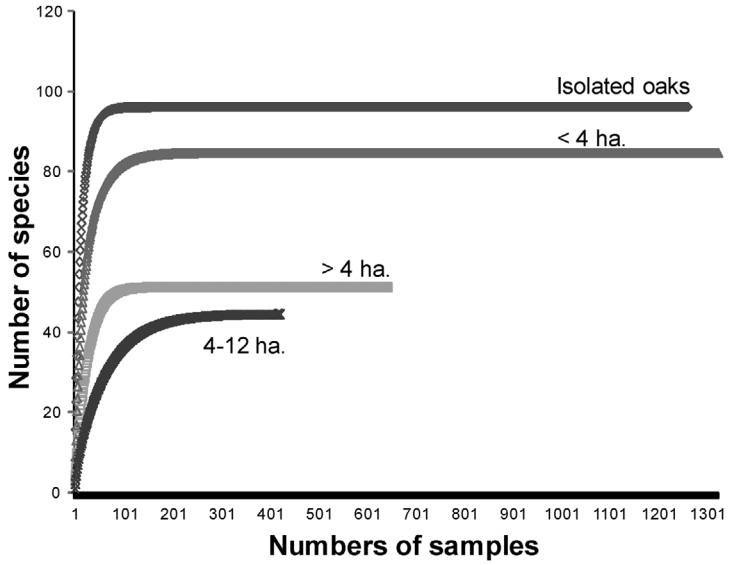

Fig. 3. Rarefaction curves plotting the number of species of gall wasps vs. the number of galls sampled.

differences in oak organ production between the interior and the edge of the fragments. Leaf production was higher at fragment edges than interiors ($F = 10.67$, df = 3, $P = 0.001$). Finally, we found a positive relationship between gall abundance and percentage of canopy cover only for isolated trees ($F = 37.4$, $R^2 = 0.61$, $P = 0.0001$). No relationship between gall abundance and percentage of canopy cover was observed in small fragments ($F = 3.2$, $R^2 = 0.12$, $P > 0.05$), medium-sized fragments ($F = 4.8$, $R^2 = 0.04$, $P > 0.05$) and large fragments ($F = 2.2$, $R^2 = 0.06$, $P > 0.05$).

Discussion

We found that both gall wasp species richness and abundance increased with habitat fragmentation. Gall wasp species richness and abundance were also higher along fragment edges that in the interior. Most strikingly, isolated oaks supported high gall wasp richness and abundance, and can thus be seen as key resources for cynipid survival and reproduction in a fragmented landscape (Chust et al. 2007, Müller and Goßner 2007).

Our results are initially counterintuitive, and contrast with the predictions of Holt's (1996) model and patterns observed in other herbivore systems (e.g., Ruiz-Guerra et al. 2010). Landscape fragmentation reduces the connectivity between patches, diminishing richness of organisms living in smaller patches due to higher rates of extinction, and reducing occupancy in the most isolated sites through low rates of recolonization (Hanski 1999). However, the extent and spatial scale of predicted fragmentation effects depend not only on structural connectivity, but also on the dispersal ability of the study species (Hanski 1999, Driscoll and Weir 2005). Species with low dispersal ability are more severely affected by fragmentation, and are the first to lose the ability to recolonize as habitat fragments become smaller and more isolated (Thomas 1995). Gall wasps, however, include highly dispersing species, and can spread a long way very quickly in air currents, even across unfavourable habitats (Hough 1951, Stone and Sunnucks 1993, Nieves-Aldrey 1995, Schönrogge et al. 2011). In this way, isolated oaks analyzed in our study, can promote the persistence of different gall wasp species along a fragmented landscape. For these reasons, we propose that oak gall wasps may have relatively high probability of locating isolated habitat fragments and isolated trees (Dauber et al. 2005). Higher frequency of encounter may also explain the high gall wasp abundance and richness at fragment edges in comparison with their interiors.

Studies that have analyzed the importance of isolated oaks on insect diversity consider them islands because they increase the survival of herbivore specialists (Chust et al. 2007, Müller and Goßner 2007). In general, isolated trees are considered keystone resources because of their ecological importance relative to their low abundance and the small area occupied (Manning et al. 2006). In tropical and temperate systems, isolated trees provide numerous ecological functions across fragmented landscapes (Ozanne et al. 2000, Manning et al. 2004). For example, canopy invertebrate arthropods, birds and mammals can all depend on isolated trees as a food resource, shelter or nesting site (Tews et al. 2004, Manning et al. 2006). Our study found isolated oaks to maintain the highest gall wasp diversity, suggesting that these trees represent keystone resources for gall wasps that contribute to their survival and reproduction in the fragmented landscape of the Lake Cuitzeo basin.

Fragmentation and host plant quality

An important finding of our study is that habitat fragmentation strongly influences host plant quality. Host quality, in terms of abundance of gall induction sites (leaves, and inference associated buds and petioles), was highest in isolated trees and in smaller forest fragments relative to larger fragments and along fragment edges relative to their interiors. We observed a similar pattern, though unquantified, for oak stems, which are also gall induction sites. We also found a positive relationship between gall abundance and canopy cover in isolated oaks. These patterns in host plant quality are entirely concordant with the observed patterns in gall wasp abundance and species richness. Even though we have not demonstrated the cause and effect relationship, the patterns observed across this set of fragments are consistent with strong bottom-up effects of host plant quality on cynipid wasp abundance and species richness (Price 1991, Preszler and Price 1995). One

possible explanation for the observed variation in plant quality may be the effect of environmental stress resulting from habitat fragmentation (Fernandes and Price 1988). Changes in abiotic conditions in forest fragments are particularly pronounced at forest edges (i.e., increased solar radiation, increased air temperature, decreased air humidity and increased wind speed) (Young and Mitchell 1994, Chen et al. 1995, Kapos et al. 1997). These changes could physiologically stress arboreal species in fragmented habitats, and cause trees to promote more frequent flowering, fruiting (Aldrich and Hamrick 1998), leaf production (Lovejoy et al. 1986, Sundarapandian and Swamy 1999) and leaf shedding (Sizer and Tanner 1999). For example, Magrach et al. (2014) indicated that some plant species show compensatory responses to habitat fragmentation involving demographic effects, and changes in plant defenses and regrowth rates. Alternatively, fragmentation may confer benefits; for example, isolated trees are free of competition from neighboring conspecifics or other species. Plant vigor may increase after disturbance because the timing of leaf abscission, leaf expansion and production is altered in these environmental conditions (Trombulak and Frissell 2000, Karban 2007).

Taken together, these host plant changes result in a greater abundance of gall induction sites for oak cynipids in isolated oaks, small fragments and forest edges. In addition, gall inducing insect radiation is expected to happen in harsh environments (e.g., xeric conditions) (Price et al. 1998, Cuevas-Reyes et al. 2004) since dry condition is known to be associated with gall richness (Price et al. 1998). Specifically, edge effect can reproduce similar conditions to those found in more xeric habitats (Fernandes and Price 1988) explaining the higher gall inducing insect richness (Murcia 1995, Araùjo et al. 2011). Stressed plants can also produce higher concentrations of chemical defense (e.g., tannins) (Müller et al. 1987, Stone et al. 2002), which decreases the frequency of other herbivores, predators and fungi and creates an enemy-free space for gall inducing insects (Fernandes and Price 1988, Fleck and Fonseca 2007).

Therefore, habitat fragmentation can favor the colonization and maintenance of gall inducing insects in comparison with other insect guilds (Ruiz-Guerra et al. 2010, Kaartinen and Roselin 2011). Some studies have shown a "crowding effect" that is a relatively positive effect of fragmentation on insect population density (Debinski and Holt 2000). After habitat fragmentation, insect populations may disperse to adjacent fragments, resulting in a local increase in population density (Debinski and Holt 2000, Grez et al. 2010) in small fragments that have a larger edge proportion (Fagan et al. 1999, Grez et al. 2010). Our results suggest a "crowding effect" of gall wasp community, in the remaining habitat as small fragments and isolated oaks.

Two further points need to be made. First, alternative correlated factors may have caused the observed patterns in gall communities. For example, habitat fragmentation may have influenced cynipid diversity through top-down effects mediated by natural enemies such as parasitoids or lethal inquilines, which can inflict high mortality on gall wasp populations (Stone et al. 2002). In small or isolated habitat fragments, phytophagous insects increase population densities when they are released from top-down control (Kruess and Tscharntke 1994, Roland and Taylor 1997). High trophic levels such as parasitoids are more affected by habitat fragmentation than herbivores (Kruess and Tscharntke 1994, Davies et al. 2000). According to theoretical (Holt et al. 1999) and empirical studies (Kruess and Tscharntke 1994, Thies and Tscharntke 1999), the main factors are that: (1) Parasitoids are more sensitive to habitat fragmentation than their hosts, because they can only colonize patches already occupied by their hosts (Weisser 2000, van Nouhuys 2005); (2) Parasitoids have smaller population sizes and depend more on recolonization processes because they suffer more from frequent disturbances and their populations are more likely to become extinct (Pimm 1991, Lawton 1995, Holt et al. 1999); (3) Habitat isolation will negatively affect parasitoids even on small spatial scales because they can disperse less well than second-trophic-level insects (Roland 1993). In this way, enemy-imposed mortality falls in smaller or more isolated fragments, resulting in ecological release of oak gall wasp populations (Holt 1996, Chust et al. 2007). If top-down forces have a strong impact on gall wasp community structure, habitat fragments could support relatively enriched gall inducer communities by providing relatively

enemy-free space. One testable explanation for our results is that habitat fragmentation indirectly affects cynipid diversity due to the decrease or disappearance of natural enemy populations (such as parasitoids and inquilines). Second, the effects of habitat fragmentation on local patterns of cynipid communities are likely to be independent of patterns at larger regional scales (e.g., Cornell 1985), paralleling patterns that have been seen in other galling herbivore communities (Araùjo et al. 2013). It remains to be seen whether the patterns described for gall inducers differ from those observed in other herbivore guilds because of specific properties of gall-associated communities (Ruiz-Guerra et al. 2010).

Oaks species as "super-hosts"

In the literature, there is a lack of studies showing that oak species can support many gall wasp species (Fernandes and Price 1988, Csóka et al. 2005). In our study, we found that three oak species (*Quercus obtusata*, *Quercus castanea* and *Quercus deserticola*) hosted 80 oak gall wasp species between them, which have been called "super-hosts" (Araùjo et al. 2013). The difference in species richness among oak species is striking, and the cause(s) of this variation require further study. It remains to be seen whether high diversity in these Mexican species reflects high net rates of speciation by specialist lineages associated with each oak, high rates of colonization by independent lineages, or a combination of both of these (Cook et al. 2002, Joy and Crespi 2007).

Given ongoing deforestation in the Lake Cuitzeo basin, it is therefore crucial to determine the critical fragmentation level (minimum fragment size, maximum fragment separation) beyond which populations of component species will collapse (Olson and Andow 2008). In recently fragmented habitats, local diversity may remain higher than the sustainable equilibrium value (supersaturation) (Boudjemadi et al. 1999), showing gradual decline in species richness with fragment age until this equilibrium is reached (Eliason and Potter 2000, Ribas et al. 2005). Our study provides a 3-year baseline of data collected using systematic and standardized sampling, on which future sampling can build to explore longer term changes in the oak gall wasp community.

Our study shows the variety of effects that habitat fragmentation exerts on remnant native populations of oak gall wasp and their host plants. We concluded that habitat fragmentation affects gall wasp diversity and plant vigor, with higher species richness, abundance and canopy cover in small fragments and isolated oaks of the Lake Cuitzeo basin, in comparison with larger fragments. Similarly, we found a positive effect of forest edge on gall richness and abundance and plant vigor. Isolated oaks can be considered keystone resources for maintaining of gall wasp species diversity in a fragmented landscape in Mexican temperate forests. Finally, in future studies, it will be important to evaluate the impact of "super-hosts" species in the insect community associated in fragmented landscapes.

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Supplemental Material

Appendix A

Table A1. Oak species present at each sampling site.

Size fragments	Site	Oak species
Smaller fragments (≤4 ha)	San José de las Torres	*Q. castanea*
	La Concepción	*Q. deserticola, Q. obtusata, Q. castanea*
	Jesús del Monte	*Q. obtusata, Q. deserticola, Q. laeta*
	Cuanajo	*Q. castanea, Q. deserticola*
	Autopista	*Q. castanea, Q. magnoliifolia*
Medium-sized fragments (4–12 ha)	Canoas	*Q. deserticola, Q. castanea*
	San José del Rincón	*Q. castanea, Q. deserticola*
	Cepamisa	*Q. castanea, Q. obtusata, Q. deserticola*
	Teremendo	*Q. castanea, Q. deserticola*
	Acuitzio	*Q. castanea, Q. obtusata, Q. deserticola*
Continuous forests (>12 ha)	Umécuaro	*Q. castanea, Q. glaucoides*
	Atécuaro	*Q. castanea, Q. candicans, Q. magnoliifolia*
	Lagunillas	*Q. castanea, Q. deserticola, Q. laeta*
	San Miguel del Monte	*Q. laeta, Q. crassifolia, Q. scythophylla, Q. castanea, Q. obtusata*
	Chiquimitio	*Q. castanea, Q. obtusata, Q. deserticola*
Isolated oaks	Isolated oaks	*Q. deserticola, Q. castanea, Q. obtusata, Q. magnoliifolia, Q. dysophylla*

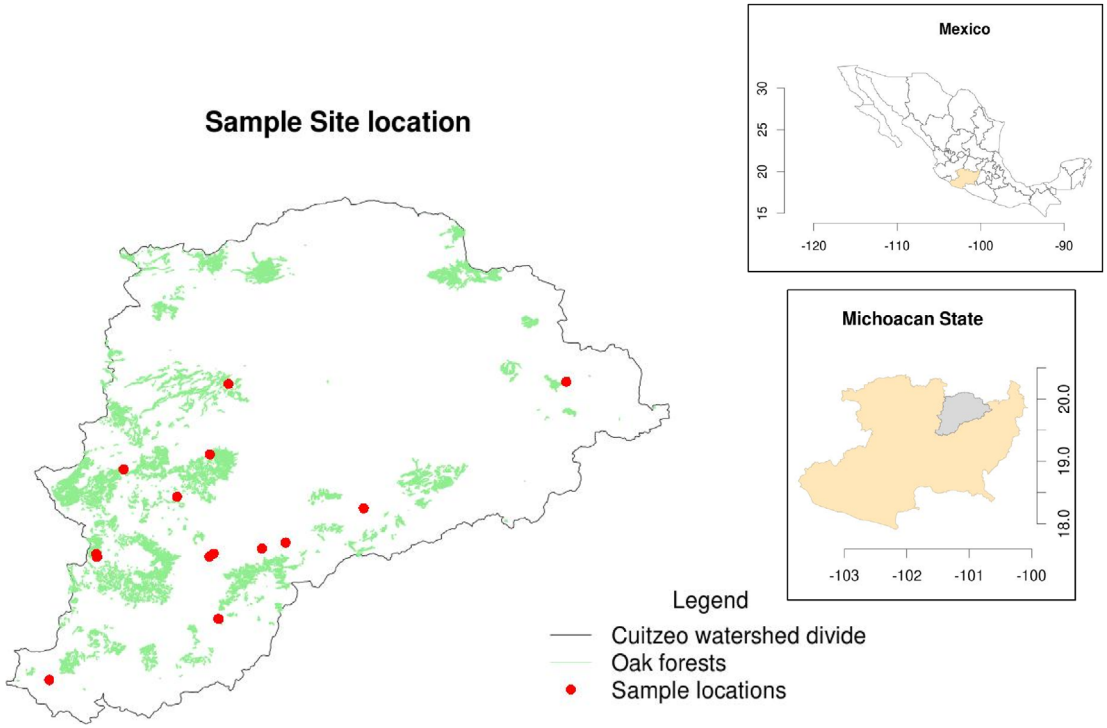

Fig. A1. Field sampling sites. The study was conducted at 15 permanent sites within the Cuitzeo basin. We selected the study sites accord to size fragments: (1) five smaller fragments (≤4 ha): San José de las Torres (19.69745, −101.060133), La Concepción (19.70943, −101.320383), Jesús del Monte (19.6506, −101.168267), Cuanajo (19.464917, −101.494733), Autopista (19.63082, −101.274083); (2) five medium-sized fragments (between 4 and 12 ha): Canoas (19.8593055, −101.2508333), San José del Rincón (19.867617, −100.779417), Cepamisa (19.63487, −101.2683), Teremendo (19.74455, −101.395217), Acuitzio (19.498786, −101.343967); and (3) five continuous forests (>12 ha): Umécuaro (1954872, −101.260333), Atécuaro (19.6423, −101.2012), Lagunillas (19.62823, −101.430917), San Miguel del Monte (19.63211, −101.431752) Chiquimitio (19.76583, −101.27531).